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A COMPARATIVE STUDY OF WINTER AND SUMMER LEAVES OF VARIOUS HERBS

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Introduction

The structure of most plants varies with the habitat and even with the varying conditions of the same habitat. This has been emphasized by GREVILLIUS,[1] CHERMEZON,[2] COWLES,[3] STARR,[4] and others. GREVILLIUS made an extensive comparative study of vegetation growing on the island Öland. He compared the plants of a dry, rocky, treeless plain (alvar) with the same species growing in favorable regions. The former he calls alvar forms; the latter, normal forms. The alvar forms, in general, were more hairy and had a more highly cutinized and thicker epidermal wall, a more compact palisade parenchyma, and more closely crowded stomata than the normal forms.

These structural peculiarities due to environmental changes may be observed readily in almost any plastic plant. *Oenothera*

[1] GREVILLIUS, A. Y., Morphologisch-anatomische Studien über die xerophile Phanerogamenvegetation der Insel Öland. Bot. Jahrb. **23**:24–108. 1897.

[2] CHERMEZON, H., Recherches anatomiques sur les plantes littorales. Ann. Sci. Nat. Bot. **12**:117–313. 1910.

[3] COWLES, H. C., The ecological relation of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. **27**:95–117, 167–202, 281–308, 361–391. 1899.

[4] STARR, ANNA M., Comparative anatomy of dune plants. BOT. GAZ. **54**: 265–305. 1912.

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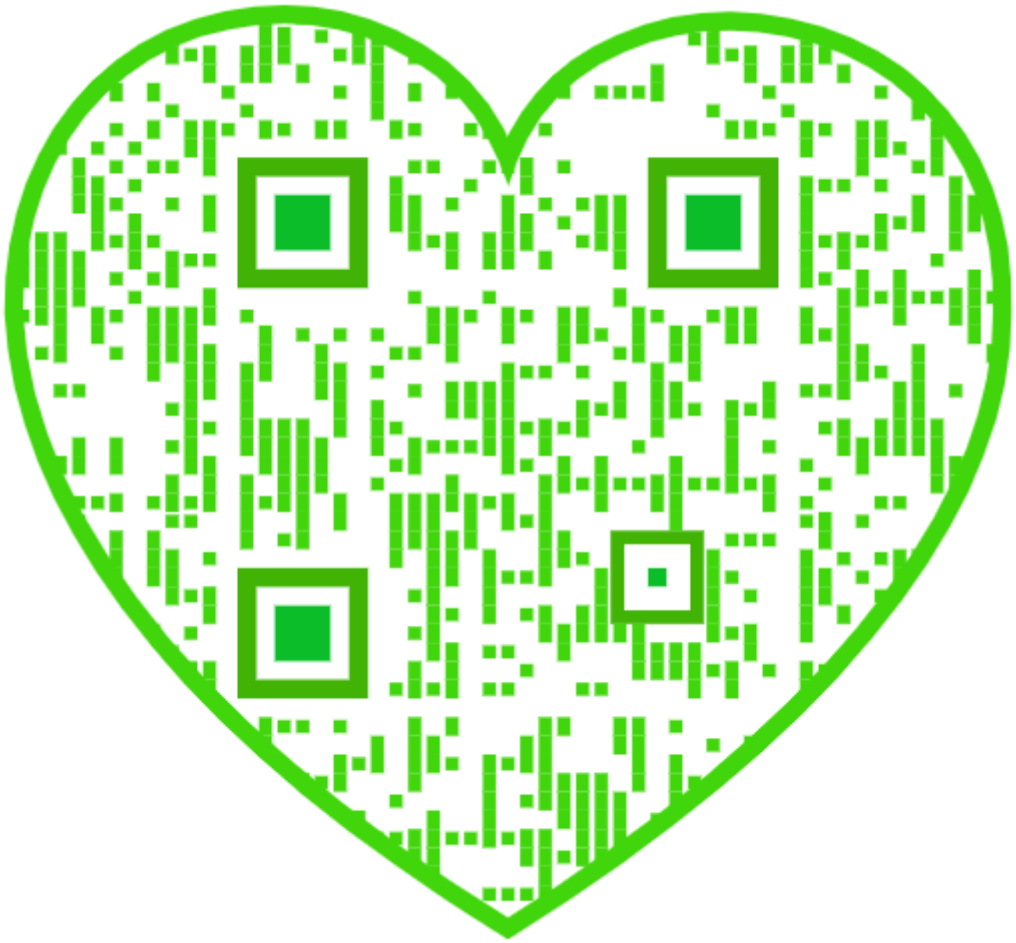

biennis, for example, when growing in a dry, sterile soil and exposed to strong wind and maximum sunlight, is found to have smaller and thicker leaves, more perfectly developed palisade parenchyma, a more hairy and a more densely cutinized epidermis, and, in general, a more xerophytic structure than the same species growing under more favorable conditions.

A similar structural difference is apparent in summer and winter leaves, or in stem and rosette leaves. Winter leaves, as the name implies, exist during the winter, which, in our latitude, is the most unfavorable season of the year. During the winter transpiration becomes relatively excessive because of the reduced rate of absorption, and plants are thus put to the severest test. Sometimes for days at a time the ground is frozen and absorption is practically zero; while during the warmest part of the day considerable transpiration may take place. The plant is thus exposed to the danger of desiccation. Moreover, during the night the most exposed leaves may freeze hard. Toward noon of the following day they may thaw out, presenting a wilted condition as if killed by scalding. However, it is surprising how quickly such leaves will revive as conditions again become more favorable. No sooner is the absorption of soil water resumed than the leaves once more become turgid and resume their wonted appearance, apparently none the worse for the ordeal through which they have passed.

Since winter leaves are exposed to such severe conditions, it would be natural to suppose that they must be quite xerophytic in structure. While this is true to a certain extent, in some respects they are less exposed to unfavorable conditions than stem leaves. This is especially true of winter leaves occurring in rosettes. In rosettes the internodes are extremely short and the leaves thus become closely crowded and overlapping. Since epinasty prevails during the winter, these overlapping leaves lie almost flat on the ground, thus affording maximum protection for each other from sudden changes of temperature, as well as from high winds and excessive transpiration. It is seldom that winter leaves die as the direct result of freezing, and when it is borne in mind that such leaves have a low water content and a high osmotic pressure, thus insuring easier absorption of soil water, the protection would seem

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ample, regardless of any special protective structures. The stem leaves, on the other hand, are usually borne some distance above the ground and exposed to greater intensity of light, stronger winds, and greater extremes in temperature, humidity, and transpiration.

Method of study

Most of the plants used in this comparative study were collected in the region about Chicago; the remainder, in eastern Pennsylvania. In order to simplify matters, all winter leaves, whether produced in typical rosettes, on prostrate runners, or on basal shoots, will be designated as rosette leaves, and summer leaves will be designated as cauline or stem leaves.

Leaves for study were killed, fixed, and preserved in a 4 per cent solution of formaldehyde in 50 per cent alcohol. Delafield's haematoxylin was used as a general staining reagent. Sections were also treated with chloriodide of zinc, the cellulose wall turning blue, while the cuticle and cutinized portions of the epidermal wall turned yellow. Alcannin tincture imparts a pink color to cutin, but is much slower in its action than chloriodide of zinc.

Unless otherwise specified, all observations were made on the middle of the leaf, from the midrib to the margin. All observations and measurements were made with $\frac{2}{3}$, $\frac{1}{6}$, and $\frac{1}{12}$ in. (oil immersion) objectives, and with a 1 in. micrometer eyepiece with divisions of 0.1 mm. Camera lucida drawings were made of portions of the epidermis for measurement and comparison of epidermal cells and stomata. Chloral hydrate was used as a clearing agent for leaves to facilitate the study of air spaces and packing of mesophyll tissues. Most measurements and counts represent an average of 5–20, depending upon the degree of variability of the objects measured. Measurements are expressed in microns, and counts represent the number in the field under low or high power, which is indicated in each case. Different plants of the same species (in cases where the plants could readily be secured) were studied at different times and the results compared. These results varied only slightly when the plants came from the same habitat, but usually differed considerably in plants from different habitats.

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With such a tendency to variation in plants, few measurements and counts can be regarded as absolutely fixed, but the final results in any case do not materially affect the principles involved.

Epidermal hairs

There is considerable variation in the kind, number, size, and distribution of epidermal hairs, not only in different plants of the same species, but also on different leaves of the same plant, or even on different parts of the same leaf. Some plants, such as *Oenothera biennis*, vary greatly when grown under different physical conditions. In a low, moist, and comparatively shady habitat the leaves of *Oenothera* are thin, and the hairs rather weak and comparatively few and scattered. On a dry slope or bank along the roadside, the leaves are decidedly thicker, and the hairs stouter and very much more abundant; while under intermediate conditions corresponding variations have been observed.

Oenothera is an extremely plastic plant, responding readily to changed conditions of environment. *Leonurus Cardiaca*, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and others also show some variations, but not to the same extent as *Oenothera*. *Verbascum Blattaria*, on the other hand, is glabrous no matter under what physical conditions it may be growing. Occasionally, when growing on a dry bank along a dusty roadside, a few hairs may be found on the ventral side of the midrib of the lower stem leaves and upper rosette leaves. This plant is extremely rigid and does not at all, or but slightly, yield to changing conditions of environment. It is perhaps a good illustration of a congenital mesophyte.

In studying the number and distribution of hairs, *Oenothera biennis*, *O. rhombipetala*, *Leonurus Cardiaca*, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and *Hieracium paniculatum* were selected as types. Care was taken to collect both the stem and rosette plant of each species in the same or as nearly the same habitat as possible. Five plants of each species were studied, and the counts for each particular kind of hairs were averaged and tabulated. The field of the low power of the microscope was adopted as the unit area of observation, and the average of 5 or more counts was taken as the number for each area under observation.

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From the tabulated results of observations made on these species of plants and a careful study of a number of other species, the following conclusions can be formulated. (1) Epidermal hairs are most abundant on the upper stem leaves, and decrease, as a rule, to the lowest stem leaves, and from the upper to the lowest rosette leaves. On the basal leaves of both stem and rosette are found the smallest number of hairs. (2) Hairs are also more abundant on the lower than on the upper surface of the leaf, usually being most abundant on the ribs, veins, and margin of the leaf. (3) Hairs are most abundant toward the base of leaves, although in basal stem and rosette leaves the reverse is usually the case. (4) Young leaves are more hairy than older ones. This may be due partly to the fact that in young immature leaves the epidermal cells have not yet reached their mature size and therefore the hairs will of necessity be more crowded than in a mature leaf. This diminished hairiness in older leaves also may be due in part to the fact that hairs in the course of time may break off, or for some reason or other drop off, and thus reduce the number per unit area of surface. (5) Exposure to sun, wind, and other desiccating influences tends to increase the hairiness in the upper stem leaves. Transpiration, wind, moisture, and character of soil are undoubtedly potent factors in determining hair production, but that these are not the only factors is clearly shown by the fact that young leaves just emerging from buds, and therefore most protected, are usually most hairy, sometimes even tomentose.

As stated before, some leaves are most hairy toward the base, where the leaf is most protected from those influences that would ordinarily tend to produce hairiness. It is difficult also to see why *Verbascum Thapsus* and *V. Blattaria* should grow side by side, the one glabrous and the other extremely hairy. So far as hairiness is concerned, it would seem that the former is a congenital xerophyte while the latter is a congenital mesophyte.

It is difficult also to see that hairiness is beneficial to plants, and that these epidermal outgrowths protect the plant against excessive transpiration, against the ravages of animals and parasites of various kinds, against excessive sunlight, etc., when *Verbascum Blattaria*, entirely devoid of hairs and with only a slightly

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thicker epidermal wall, is fully as successful in the struggle for existence as *V. Thapsus* growing by its side, so thoroughly protected by an abundance of epidermal hairs. It is not difficult to see that the woolly coating may be advantageous to young leaves, just emerging from the bud; but it is extremely difficult to find any advantage in the few simple and stellate hairs scattered over the leaves of *Lepidium* and *Capsella.*

Stomata

In over two-thirds of all the plants studied the stomata were found to be more abundant on stem than on rosette leaves. Sometimes this difference in number is only slight, but sometimes, as in *Mitella diphylla*, *Lepidium virginicum*, *Monarda punctata*, *Aquilegia canadensis*, *Campanula rotundifolia*, *Capsella Bursa-pastoris*, and *Geum album*, this difference is considerable. Stomata are also most abundant on the lower side of the leaf. This is true of about 80 per cent of all the plants studied. This difference is most pronounced in leaves that have their upper and lower sides well developed, such as the broad mesophytic rosette leaves. Narrow, xerophytic stem leaves, such as have both sides almost equally exposed to light and air, have approximately the same number of stomata on both sides. The more xerophytic the leaves, the greater are the number of stomata as compared with the corresponding mesophytic leaves. As a rule, the size of stomata is correlated with the number. The larger the number of stomata on a given leaf surface the smaller they are. This was found to be true in over 60 per cent of the specimens compared. Broad mesophytic rosette leaves have fewer but larger stomata on a given surface than the corresponding narrower, more xerophytic stem leaves. In these there is a larger number of stomata per unit surface, but the stomata are decidedly smaller in size.

There also seems to be a correlation between the number and size of stomata, and the size of epidermal cells. The broad rosette leaves have, as a rule, larger epidermal cells. With these larger cells are associated fewer but larger stomata.

Anterior-posterior orientation of stomata is noticeable in the stem leaves of *Campanula rotundifolia*, *Linaria canadensis*, *Arabis*

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lyrata, *A. brachycarpa*, *A. laevigata*, and *Satureja glabra;* and in both stem and rosette leaves of *Artemisia caudata* and *Lechea villosa*. All these leaves are linear or oblong. Not all linear or oblong leaves have their stomata longitudinally oriented, but such orientation is characteristic of linear and oblong leaves, especially if the epidermal cells are longitudinally elongated.

The stomata of the species investigated are not sunken below the surface in either stem or rosette leaves, except in the sand dune xerophytes, *Artemisia canadensis* and *A. caudata*, where they are depressed about half the thickness of the epidermis. In a few instances the stomata seemed even to be elevated slightly above the surface. In *Mitella diphylla*, *Leonurus Cardiaca*, *Aquilegia canadensis*, and *Chelidonium majus*, the stomata are confined to the ventral surface of the leaf.

Rosette stomata are not only larger but also more elongated than stem stomata. Stem stomata are not only smaller but also more nearly round than rosette stomata. Perhaps the number of stomata ought to be correlated with the mass of the chlorenchyma. The smaller number of stomata in the broad, thin (frequently thicker than stem leaves), mesophytic rosette leaves, when compared with the smaller mass of chlorenchyma to be aerated, may be relatively as abundant as the larger number per unit surface in the long, narrow, thick xerophytic stem leaves, where a larger mass of chlorenchyma must be aerated through a given surface area; that is, the number of stomata is correlated with the amount of chlorenchyma to be aerated, and not with the mere surface area of the leaf. The number of stomata also seems to be correlated with the thickness of the cuticle and cutinized outer wall of the epidermis. The greater the thickness, the less is the possibility of gases passing through, and the greater is the need for stomata. It is probably for these two reasons, the greater mass of chlorenchyma per leaf surface and the greater thickness of the cuticle and cutinized outer wall of the epidermal cells, that xerophytic leaves have an increased number of stomata in a given surface area. The relatively thinner and frequently more shaded rosette leaves are broader and have a thinner cuticle, a thinner outer epidermal wall, and a greater development of air

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lacunae. Such leaves need fewer and are provided with a smaller number of stomata. Stomata are not needed for transpiration, since transpiration is believed to be a necessary evil. It seems strange, therefore, that in xerophytic leaves, where there is effected the greatest protection against the loss of water by the development of a thick cuticle and a thick outer epidermal wall, there should be the development of a large number of stomata, thus facilitating the loss of water from the plant through stomatal transpiration.

In leaves whose outer epidermal wall and cuticle are thin, there is less need of stomata to facilitate exchange of gases in photosynthesis and respiration, since under such circumstances considerable interchange of gases can take place through the epidermis. There is no doubt that mesophytic rosette leaves with a reduced number of stomata have an ample supply of stomata to meet their needs. Moreover, rosette leaves are close to the soil and are therefore more advantageously situated for the intake of carbon dioxide than are stem leaves. In stem leaves the pressure of CO_2 cannot accumulate beyond 0.0003 A, or about 0.22 mm. Hg, since above this pressure it diffuses outward. But in rosette leaves close to the ground, where the exhalation of CO_2 from the soil often increases the CO_2 to 10 or more times the normal amount, a much higher pressure of CO_2 may accumulate. This increased amount of CO_2 in rosette leaves is available for carbohydrate synthesis in all cases where the leaves are not too much shaded. But since plants under normal conditions receive much more energy of sunlight (about 4 or 5 times as much) than is necessary to synthesize the small amount of available CO_2, rosette leaves are most advantageously situated for photosynthesis in spite of the reduced number of stomata and the diminished amount of light. These facts have an important bearing upon the development of chlorenchyma and air spaces in rosette leaves.

Epidermal cells

In monocotyledonous plants the epidermal cells are usually elongated. In dicotyledonous plants they are generally elongated along the ribs and larger veins, but elsewhere they may be polygonal and nearly isodiametric in outline, or entirely irregular. The

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shape of the leaf, to a certain extent, determines the shape of the epidermal cells. In narrow and elongated, or linear, leaves, such as those of the stems of *Arabis brachycarpa*, *A. lyrata*, *Linaria villosa*, and *Artemisia caudata*, the epidermal cells also are elongated or linear. In such elongated or linear cells the lateral walls are quite regular. The upper epidermal cells, however, are usually more regular than the lower, except in such stem or rosette leaves as are almost equally exposed to light. Such leaves have both surfaces almost equally exposed to desiccating influences, hence the shape and size of the epidermal cells on both sides of the leaf are practically the same. This is very apparent in such xerophytic stem leaves as those of *Linaria villosa*, *Arabis lyrata*, *A. brachycarpa*, *A. laevigata*, and *Campanula rotundifolia*.

The shape and size of epidermal cells vary greatly, not only in different species and in individuals of the same species, but even in stem and rosette leaves of the same individual. There may even occur considerable variation in different parts of the same leaf. Thus in *Leonurus Cardiaca* the sinuosity of the lateral walls increases slightly from the lower to the upper stem leaves. In *Geum album* the sinuosity seems to increase from the upper to the lower rosette leaves. In *Lepidium virginicum* the sinuosity is practically the same from the upper stem leaves to the lowest rosette leaves. However, the sinuosity in the lower epidermis, in the case of *Lepidium*, is greater than in the upper epidermis. The lateral walls of the lower epidermal cells are, as a rule, more sinuous than those of the upper epidermis, and in the majority of instances (70 per cent) the sinuosity is greater in rosette than in stem leaves. Sinuosity of the lateral wall culminates under the most mesophytic conditions. Increased transpiration tends to produce relatively straight lateral walls. Hence we find the epidermal walls of the stem leaves less sinuous than those of rosette leaves, and those of the upper surface of both stem and rosette leaves less sinuous than those of the lower surface, since stem leaves are more xerophytic than rosette leaves, and the upper side of leaves more xerophytic than the lower side. Sinuosity of lateral epidermal walls is not known to be of special significance to plants. It may add a little to the strength of the epidermis and afford a larger diffusion surface

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for substances passing from cell to cell. No chloroplasts are present in epidermal cells except in guard cells, and, to a slight extent, in winter leaves of *Leonurus Cardiaca*.

As to size, the upper epidermal cells are larger than the lower, and, with few exceptions, the epidermal cells of rosette leaves are larger than those of stem leaves. In 80 per cent of all observations made the epidermal cells of rosette leaves were found to be larger than those of stem leaves. The size of epidermal cells is somewhat correlated with the size of leaves, the larger leaves having the larger epidermal cells; but there are so many exceptions to this that such a general statement is not warranted.

The vertical diameter of epidermal cells is greater, as a rule, in rosette than in stem leaves (true of 80 per cent of cases), in the upper than in the lower epidermis, and usually increases from the apex toward the base of the leaf. In the middle rosette leaves the maximum diameter is usually found in the middle of the leaf. In *Capsella* there is a gradual increase from the upper stem to the lowest rosette leaves. As a rule, the maximum diameter is attained in both the middle stem and rosette leaves.

Blade, epidermal wall, and cuticle

The blade decreases in thickness from the apex to the base of the leaf. It also decreases from the upper to the basal leaves. This is less apparent in middle leaves, where the leaf sometimes increases in thickness from apex to base, or where the maximum thickness of the blade occurs in the middle of the leaf. Those leaves or parts of leaves most shaded are usually thinnest. Rosette leaves are thicker than stem leaves, owing to a greater development of spongy parenchyma. This is true more particularly of the middle and basal stem and rosette leaves. The upper stem leaves, especially the apical portions of those leaves, are frequently thicker than the corresponding portions of rosette leaves. The blade, in most instances, also appears thicker than the blades of stem leaves. Notable exceptions are *Arabis lyrata*, *A. laevigata*, *Linaria canadensis*, *Leonurus Cardiaca*, *Campanula rotundifolia*, and *Monarda punctata*. All these species, except *Leonurus Cardiaca*, have either linear or oblong lanceolate stem leaves, while the basal leaves

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are broad and thin. These are plants that have almost a typical xerophytic shoot and a mesophytic rosette.

The outer epidermal wall is decidedly thicker in stem than in rosette leaves. In each of the 3 types considered, *Lepidium virginicum*, *Capsella Bursa-pastoris*, and *Chrysanthemum Leucanthemum*, the stem leaves are borne considerably above the ground and rather widely separated from each other, thus exposing them freely to air, sunlight, and desiccating winds. The rosette leaves, on the other hand, are close to the ground and considerably shaded; hence we should naturally expect this difference in thickness of epidermal cell walls. There is a slight tendency for the wall to diminish in thickness from the apex to the base of the leaf. The maximum thickness is usually reached in middle stem and apical rosette leaves, while the maximum thinness is probably to be found in the lowest rosette leaves. The outer epidermal wall on the upper surface of the stem leaves is but slightly thicker than that of the lower, especially in those upper stem leaves that grow obliquely upward so as to expose both surfaces almost equally. In the lower stem and rosette leaves this difference is much greater, the epidermal wall on the lower side being considerably thinner. The thickness of the cuticle varies with the thickness of the outer epidermal wall, the thickest wall having the thickest cuticle. The cuticle of the stem leaves of the types treated is decidedly thicker than that in the rosette leaves. It is thicker on the upper than on the lower surface of the leaf, except in the upper stem leaves, where both surfaces are about equally exposed. Here the lower cuticle is almost as well developed as the upper. The greatest decrease in thickness of cuticle is observable in the basal rosette leaves.

In interpreting the facts set forth it must be borne in mind that only middle stem leaves are compared with middle rosette leaves, and that whatever conclusions may be deduced must rest upon this comparison. Most plants have their rosettes better protected than their shoots. In 83 per cent of 30 plants observed, the cuticle is thicker in rosette than in stem leaves. In at least 75 per cent of the number the epidermal wall is also thicker in rosette than in stem leaves. Thus it seems that when the effective means of

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protection of the middle stem leaves and the middle rosette leaves are compared, the preponderance of protection is in favor of the rosette leaves. However, it must be borne in mind that the difference in thickness of wall and cuticle in a number of instances is so slight as to be almost negligible. Moreover, in notable instances the stem leaves have a decidedly thicker wall and cuticle. This is true of *Chrysanthemum Leucanthemum*, *Capsella Bursa-pastoris*, *Artemisia caudata*, *Satureja glabra*, *Scutellaria parvula*, and others. *Chrysanthemum* has broad, spatulate rosette leaves on long slender petioles, while the stem leaves are oblong or oblanceolate, and have a decidedly xerophytic form and structure. The stem leaves of *Lepidium*, *Capsella*, *Satureja*, and, to a certain extent, *Scutellaria*, in like manner have a decidedly xerophytic form and structure as compared with their corresponding rosette leaves. *Artemisia* is one of those sand dune xerophytes whose stem and rosette leaves are finely dissected and almost equally exposed, and hence almost equally xerophytic in form and structure. In such mesoxerophytes as *Verbascum Thapsus*, whose leaves are thoroughly protected by a woolly coat of branching multicellular hairs, the difference in protection of stem and rosette leaves is also slight. Some plants, therefore, seem to have xerophytic shoots and mesophytic rosettes; others show a tendency to xerophytic rosettes and mesophytic shoots; while in still others the distinction is not evident.

Chlorenchyma

The apical, middle, and basal stem and rosette leaves of certain plants were studied with a view to determining the similarities and differences of the chlorenchyma of the corresponding regions of the stem and rosette leaves of the same plant. For example, an apical stem leaf and an apical rosette leaf would be selected for comparative study. Sections through the apical region of the stem leaf were then studied and the results compared with those obtained from a similar study of corresponding sections of the rosette leaf. Sections through the middle and basal regions of the leaves were similarly studied and compared. After the apical leaves were thus studied, the middle stem and middle rosette leaves, as well as the basal stem and basal rosette leaves, were similarly

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studied. The thickness of the leaf, the thickness of the palisade parenchyma, the thickness of the spongy parenchyma, the number of the palisade layers of cells, and the average size of the cells of each layer, together with the size, shape, and arrangement of the cells of the spongy parenchyma, were the leading points of observation in this comparative study. All measurements are expressed in microns, and were made approximately 800 μ from the midrib of the leaf. For want of space the tabulated results cannot be given; a general summary in each case must suffice.

LEPIDIUM VIRGINICUM.—In the upper stem leaves the palisade parenchyma is almost equally developed in both the upper and lower side of the leaf. This may be due to the fact that the leaves stand at a very acute angle to the stem and are almost equally illuminated. In the middle stem leaves a lower palisade tissue is found only in the apical region of the leaf. No lower palisade layers are found in the lower stem leaves or in any of the rosette leaves. The palisade layers of the upper stem leaves are quite compact. The cells reach a maximum length in the middle stem leaves. In the basal stem leaves the cells become larger and more rounded, the layers are less closely packed and less definitely organized. The palisade cells of the rosette leaves are larger, having a decidedly greater diameter, and on the whole are less compactly arranged than in stem leaves. The upper and middle stem leaves have the thickest outer epidermal wall and cuticle. This is also true of the upper rosette leaves when compared with the lower. The difference, however, between the thickness of the epidermal wall and cuticle of the apical and basal leaves is much greater in rosette than in stem leaves.

CAPSELLA BURSA-PASTORIS.—The outer epidermal wall of stem leaves is thicker in the upper than in the basal leaves, attaining a maximum in the middle leaves. The cuticle is proportionally thickest in the upper leaves and thinnest in the proximal part of the basal leaves. Similar conditions obtain in the rosette leaves, except that the contrast between apical and basal cells is less pronounced. Palisade tissue is best developed in both upper stem and upper rosette leaves. Palisade cells are slightly longer and decidedly thicker in rosette than in stem leaves. The cells of the

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spongy parenchyma are decidedly more irregular in rosette leaves, and the tissue contains a maximum of air spaces. Palisade tissue is least developed in basal stem and rosette leaves, as well as in the basal region of the leaves themselves.

CHRYSANTHEMUM LEUCANTHEMUM.—The outer epidermal wall and cuticle of the upper and middle stem leaves are very much alike in thickness, but both are decidedly thicker than the corresponding epidermal wall and cuticle of the basal stem leaves, the latter being only about one-half as thick. Rosette leaves do not differ much from each other in the thickness of epidermal wall and cuticle, but the maximum thickness may probably be found in the middle leaf. Rosette leaves, as a whole, have a thinner epidermal wall and cuticle than stem leaves, being only one-half to two-thirds as thick. The palisade tissue is better developed, as a whole, in stem than in rosette leaves, and decidedly better developed in both stem and rosette leaves in apical and middle leaves than in basal leaves. The spongy parenchyma is slightly better developed in rosette leaves and in both kinds of basal leaves. Here is found also the maximum development of air spaces.

OENOTHERA BIENNIS.—The stem leaves are thickest in the apical region and gradually become thinner toward the base. There is also a gradual increase in thickness from the apical to the basal stem leaves. The upper rosette leaves are thickest in the apical region and become thin toward the base of the leaf. In the middle and lower rosette leaves the greatest thickness is found in the middle region. From this region they gradually become thinner toward both the apex and base of the leaf.

The spongy parenchyma in stem leaves gradually diminishes from the apical to the basal region of the leaf, but there is a gradual increase in amount from the apical to the basal leaves. In the upper rosette leaves the spongy parenchyma also gradually decreases from the apex of the leaf to the base. In the middle and lower rosette leaves, however, the greatest percentage of spongy tissue is found in the apical and basal regions. In stem leaves the palisade tissue is most developed in the apical region and least in the basal region. The maximum development is probably found

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in the apical and middle regions of the basal leaves. The palisade cells of rosette leaves are decidedly broader or thicker than those in stem leaves, but are relatively slightly longer. The maximum development is found in the apical and middle regions of the leaf, or in those parts of the leaves having the greatest exposure to light and other desiccating influences.

The largest epidermal cells are found in the middle region of both stem and rosette leaves. It is also in the middle of leaves that both upper and lower epidermal cells have the greatest vertical diameter. The outer epidermal wall and cuticle of stem leaves are thickest in the apical leaves, and gradually become thinner toward the basal leaves. In the upper stem leaves the outer wall and cuticle diminish from the apical to the basal region. In the middle and basal stem leaves there is less difference, and in the lowest leaves there is practically no difference in thickness of the epidermal wall and cuticle in different regions. In the upper stem leaves there is not much difference in the thickness of the epidermal wall and cuticle of the upper and lower sides of the leaf; but in the lower stem leaves the thickness is decidedly greater in the upper than in the lower epidermis. The greatest difference in thickness is found in the lowest leaves.

In rosette leaves the situation in thickness of epidermal wall and cuticle is similar to that found in stem leaves. In the upper rosette leaves, however, there is a greater difference in thickness of wall and cuticle between the apical and basal regions of the leaf. The hairs on both stem and rosette leaves are longest and most abundant on the midrib and have larger veins than elsewhere. The hairs are most abundant on the upper stem leaves and gradually diminish in number and size to the basal leaves, where they are quite small (except on veins) and only half or even less than half, as abundant. On the upper leaves they are longer and more abundant on the lower than on the upper surface, and increase in length and abundance from the apex to the base. On the middle stem leaves they are similar in size and abundance on both sides of the leaf, but slightly decrease in number from apex to base. On the basal leaves the hairs are considerably reduced in size, but otherwise the situation is similar to that found in middle stem

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leaves. On rosette leaves the hairs are slightly more abundant on the upper than on the lower surface, and gradually diminish in size and number toward the basal leaves. On the lower side of the basal leaves there are very few hairs except along the margin, where they are long and abundant. The chlorenchyma contains an abundance of needle-shaped crystals of calcium oxalate, arranged in bundles (raphides). These raphides are slightly more abundant in rosette than in stem leaves.

VERBASCUM BLATTARIA.—In this species the palisade tissue is best developed in the floral leaflets and in the upper stem leaves. Here the layers are well organized and compact, and the cells reach their maximum length. In the basal stem leaves the palisade cells vary considerably in length, some being quite long, while others are quite short. Moreover, the layers are poorly organized. In the middle and upper stem leaves 3 layers are well organized, a fourth layer being only partly organized. In the basal leaves there is no trace of a fourth layer. The thickness, or transverse diameter of the palisade cells, also increases appreciably from the upper to the lowest stem-leaves. In rosette leaves there is a gradual increase in the size of palisade cells from the upper to the basal leaves. In the latter the palisade tissue is poorly developed, the cells being very irregularly and loosely arranged, and scantily supplied with chloroplasts.

With the exception of a few hairs on the ribs of rosette leaves and lowest stem leaves, this plant is devoid of hairs. The basal stem leaves and rosette leaves have the largest epidermal cells, which also have the largest vertical diameter. The upper epidermal cells of both stem and rosette leaves always have a decidedly greater vertical diameter than the cells of the lower epidermis.

The floral leaflets and upper stem leaves have the thickest outer epidermal wall and cuticle. In these leaves there is very little difference between the upper and lower epidermis. In the upper rosette leaves we also find a thicker epidermal wall and cuticle, but the difference is less pronounced than in stem leaves.

A summary of the comparative study of the upper, middle, and lower stem leaves and the corresponding upper, middle, and lower rosette leaves, based upon the 5 species just considered,

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and in addition *Leonurus Cardiaca* and *Verbascum Thapsus*, is as follows.

In general the lowest stem and rosette leaves, as well as the basal part of all leaves, are most protected and most shaded, and therefore have the most mesophytic structure. The leaves are thinnest; the outer epidermal wall and cuticle are thinnest; the palisade parenchyma is developed most poorly; and spongy parenchyma, containing a maximum of air spaces and a minimum of chloroplasts, is developed most highly.

The upper stem leaves are relatively xerophytic in structure. This is especially true of the apical region of these leaves. We frequently find the maximum thickness of leaf, maximum thickness of epidermal wall and cuticle, and a maximum development of palisade tissue, which in many instances develops almost equally on both sides of the leaf. The middle and lower stem leaves are almost invariably thinner than the corresponding rosette leaves. The spongy parenchyma is better developed in rosette than in stem leaves. This was true of 75 per cent of all sections studied.

The palisade parenchyma in stem leaves is better organized, more compact, and the cells relatively longer and narrower as compared with the thickness of the leaf. In rosette leaves the layers of palisade tissue are frequently less perfectly organized, less compact, and the cells larger. Palisade cells of rosette leaves are decidedly broader and usually longer than those of stem leaves; but the amount of palisade tissue and the length of the cells, when compared with the average thickness of the leaves, are less in rosette than in stem leaves. The absolute length of palisade cells in the first layer is greater in rosette leaves than in corresponding stem leaves in 70 per cent, in the second layer in 55 per cent, and in the third layer in 28 per cent of all sections studied. In 30 per cent of all stem sections studied the second palisade layer was not developed. The same was found to be the case in 29 per cent of rosette sections studied. Likewise, the third palisade layer was not developed in 81 per cent of all stem sections studied, or in 66 per cent of all rosette sections studied. The number of sections considered in each case was the same (75 stem and 75 rosette sections). With the exception of the upper stem leaves, where the

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upper and lower epidermis frequently have an outer wall of approximately equal thickness the upper epidermis has a thicker wall than the lower. In 93 per cent of the cases the outer epidermal wall and cuticle of stem leaves were found to be thicker in stem than in rosette leaves. The thickest epidermal walls are usually found in the outer two-thirds of upper stem leaves. On the other hand, rosette leaves have epidermal cells with the largest vertical diameter and contain a maximum of air spaces.

Lepidium virginicum and *Capsella Bursa-pastoris* produce both summer and winter rosettes. When these rosettes are compared, it is found that summer rosettes have slightly thicker leaves (thinner in *Capsella*), a thicker cuticle, and a thicker outer epidermal wall. The palisade parenchyma also is better developed. There are frequently more layers, and the cells are longer and narrower. These differences are most pronounced in *Lepidium*.

SUMMARY ON CHLORENCHYMA.—Typical xerophytic leaves have a relatively compact and well developed palisade tissue; also a relatively small amount of spongy parenchyma with small air spaces. The mechanical tissue is usually also better developed than in mesophytic and shade leaves. Since rosette leaves are usually broad, close to the ground, frequently more or less shaded, and therefore in most respects better protected than stem leaves, it should not be surprising if the former were found to be more mesophytic than the latter. That this seems to be true, at least of the forms studied, is shown by the following deductions.

1. Rosette leaves, as a rule, have a greater amount of chlorenchyma than stem leaves. This is true of at least 80 per cent of all plants studied.

2. Rosette leaves have a greater amount of spongy parenchyma than stem leaves, although the percentage of the chlorenchyma is slightly greater in the latter than in the former.

3. The percentage of air spaces in both palisade and spongy parenchyma is also greater in rosette than in stem leaves. This is true of about 86 per cent of all plants studied. In a considerable number of instances, however, the differences are slight.

4. The number of palisade layers is much the same in both kinds of leaves, but the average length of palisade cells, in at least

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80 per cent of the types studied, is greater in rosette than in stem leaves. This is correlated perhaps with the greater thickness of the chlorenchyma in the former. The thickness of palisade cells, in at least 90 per cent of all cases, is also greater in rosette than in stem leaves.

5. The average size of spongy parenchyma cells is also greater in rosette than in stem leaves. This is true of about 90 per cent of all plants studied.

6. Sclerenchyma tissue seems to be about equally well developed in ribs and veins of both kinds of leaves. The conductive tubes in veins of approximately equal size have a slightly larger lumen and a wall slightly thicker in rosette than in stem leaves. The conductive system of rosette leaves is better developed in rosette than in stem leaves, although this rule is not without exceptions.

On the whole, therefore, it may be said that, so far as the structure of chlorenchyma is concerned, stem leaves are more xerophytic in structure than rosette leaves, although the latter appear to be more xerophytic so far as the greater thickness of epidermal wall and cuticle are concerned. In some instances the xerophytic character of stem leaves, as compared with the rosette leaves of the same plant, is so pronounced as to be easily detected with the naked eye.

Conclusions

1. Hairs are most abundant in the upper stem leaves and decrease to the basal leaves; they are also most abundant in the upper rosette leaves and decrease to the basal leaves. In general, however, the stem leaves are more hairy than the rosette leaves.

2. Stomata are usually smaller, more nearly round, and more abundant, per unit area, on stem than on rosette leaves.

3. As a rule, the epidermal cells of rosette leaves are larger than those of stem leaves and have more sinuous lateral walls. The shape of the cells is usually correlated with the shape of the leaf.

4. The blade of rosette leaves is thicker than that of stem leaves, chiefly owing to a greater development of spongy parenchyma. This is not true, however, of stem leaves that are long,

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narrow, and of a decidedly xerophytic form and structure as compared with rosette leaves.

5. The outer epidermal wall of rosette leaves is thicker, as a rule, than in stem leaves. The maximum thickness occurs in middle stem and apical rosette leaves. The thickness of the cuticle varies with the thickness of the epidermal wall, the thickest walls having the thickest cuticle. Rosette leaves in the large majority of instances have the thickest cuticle. The preponderance of epidermal protection is in favor of rosette leaves. In stem leaves of xerophytic form the preponderance of epidermal protection is in favor of stem leaves.

6. In a comparison of the different stem and rosette leaves of the same plant it is obvious that the lowest stem and lowest rosette leaves, as well as the basal part of all leaves, have the thinnest epidermal wall, thinnest cuticle, the most poorly developed palisade tissue, the maximum development of spongy tissue and air spaces, and the minimum development of chloroplasts. The upper stem leaves are relatively xerophytic in structure, especially in the apical region of these leaves. The middle and lower stem leaves are usually thinner than the corresponding rosette leaves. The palisade parenchyma in stem leaves usually is better organized, more compact, and the cells relatively longer and narrower, as compared with the thickness of the leaf, than in rosette leaves. The thickness of palisade cells of rosette leaves is greater, in most cases, than in stem leaves. This is also true of the absolute length in the great majority of instances.

7. When the chlorenchyma in middle stem and middle rosette leaves is compared we may conclude: (1) that rosette leaves, in most cases, have a greater amount of chlorenchyma than stem leaves (this is especially true of spongy parenchyma); (2) that in most cases rosette leaves also have more air spaces than stem leaves; (3) that there is little difference in the number of palisade layers in the two kinds of leaves, but in most cases the absolute size of the palisade cells (length and thickness) is greater in rosette than in stem leaves; (4) that the average size of cells of the spongy parenchyma is also greater in rosette than in stem leaves; (5) that sclerenchyma tissue is about equally developed in both kinds of

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leaves, but the conductive tissue is slightly better developed in rosette than in stem leaves.

On the whole, typical rosette leaves, where there is considerable shading and protection, are decidedly more mesophytic than stem leaves. In winter leaves on stolons or runners there is a tendency toward greater xerophytism than in stem leaves, but on the whole the rosette leaves are more mesophytic in structure than stem leaves.

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